

FIRST RECORD OF AN EXTANT, SIGHTED, SHALLOW-WATER  
SPECIES OF THE GENUS *POSEIDONAMICUS* BENSON  
(OSTRACODA) FROM THE CONTINENTAL MARGIN OF  
SOUTH-WESTERN AFRICA

By

R. C. WHATLEY

*Department of Geology, University College, Aberystwyth, UK*

&

R. V. DINGLE

*South African Museum, Cape Town*

(With 11 figures and 3 tables)

[MS accepted 23 August 1988]

ABSTRACT

A new, sighted species of the ostracod genus *Poseidonamicus* (*P. panopsus* sp. nov.) is recorded living on the continental shelf and upper slope off south-western Africa in water depths between 120 m and 545 m. All previous records of the genus have been from water depths greater than 1 km. The discovery indicates that sighted species survived, in shallow-water, from the late Cretaceous/early Tertiary stocks when the genus originated in the SW Pacific area. The habitat of the new species is defined in terms of temperature, salinity, and dissolved oxygen values within the Antarctic Intermediate Water mass, where it forms part of the Benguela system, and associated cells of intense upwelling.

CONTENTS

	PAGE
Introduction .....	437
Taxonomy .....	438
Discussion .....	447
Distribution and ecology .....	448
General considerations .....	454
Acknowledgements .....	456
References .....	456

INTRODUCTION

Cenozoic bathyal and abyssal deep-water ostracod faunas are characterized by distinctive cosmopolitan assemblages that include a number of ornate cytheracean taxa. Prominent amongst this group is the genus *Poseidonamicus*, which was originally erected by Benson (1972) to accommodate five species with a geological range ?Oligocene, Miocene-Recent, and which is extant

world-wide (Table 1). All the original species considered by Benson (1972), as well as two further Miocene species from the South Atlantic (Benson in Benson & Peypouquet 1983), were blind. Subsequent studies by Whatley and his colleagues (e.g. Whatley 1983, 1985; Whatley *et al.* 1983; Whatley *et al.* 1986) have extended the geological and geographical range of the genus (now known from Eocene to Recent). Despite the fact that Whatley *et al.* (1986) described one species with distinct but non-functional ocular structures (*P. ocularis* Whatley *et al.* 1986), all records of the genus to date have been from water depths known or estimated to be in excess of 1 km. *Poseidonamicus* has, therefore, up to now been considered typically a deep-water taxon, although the discovery of *P. ocularis* in Quaternary deep-water sediments prompted Whatley *et al.* (1986) to predict that a shallow-water ancestor existed at least until late Tertiary times in the SW Pacific region.

Table 1 lists the known species of the genus *Poseidonamicus*, as well as their geological and geographical ranges.

The most widely recorded species to date has been the type species *P. major* Benson, which has a known geological range Miocene to Recent (southern hemisphere), and a possible record in Oligocene of the NE Atlantic (Table 1). This species occurs in Pleistocene–Recent sediments off south-western Africa, where it has a known depth range 2 070–2 916 m (Dingle *et al.* in press).

Although the genus has been recorded from Tertiary sediments in the South Atlantic (*P. riograndensis* and *P. miocenica* from the Miocene of Deep Sea Drilling Project (DSDP) site 92—Benson & Peypouquet 1983), the main centre of evolutionary activity and the area where the genus has the longest geological record (Eocene to Recent) is the SW Pacific (e.g. Whatley 1985). No positive identifications of the genus have so far been made in the Tertiary strata of southern Africa (Frewin's 1987 record is considered questionable), so that the discovery of an extant population of a shallow-water species off southern Africa poses some interesting evolutionary, zoogeographical, and environmental questions.

A total of 119 valves of the new species (*P. panopsus*) have been recovered in 27 sediment samples from the continental shelf and slope off south-western Africa (Fig. 1, Table 2). All the samples were collected with a Van Veen grab by the Marine Geoscience Unit of the University of Cape Town from the research vessel *Thomas B. Davie*. (Sample numbers have a TBD prefix.)

#### TAXONOMY

All illustrated material is housed in the South African Museum under catalogue numbers prefixed SAM-PQ-MF. Abbreviations: ACA = anterior cardinal angle, AM = anterior margin, ATE = anterior terminal element, DM = dorsal margin, LV = left valve, MS = muscle scars, PM = posterior margin, PTE = posterior terminal element, RV = right valve, SCT = subcentral tubercle, VM = ventral margin.

TABLE 1  
Spatial and temporal distribution of previously described species of *Poseidonamicus*.

Species	Age	Locality	Depth	Reference
<i>Poseidonamicus major</i> Benson, 1972	?Oligocene Miocene--Recent Miocene--?Recent Recent Quaternary	NE Atlantic SW Pacific SW Atlantic SW Indian SE Atlantic	bathyal--abyssal abyssal abyssal	Benson (1972) Benson (1972) Benson (1972) Benson (1972) Dingle, Lord & Boomer (in press)
<i>Poseidonamicus minor</i> Benson, 1972	Quaternary	E Pacific		Benson (1972)
<i>Poseidonamicus nudus</i> Benson, 1972	Recent	Indian, SE Pacific		Benson (1972)
<i>Poseidonamicus pintoii</i> Benson, 1972	Recent	S Atlantic		Benson (1972)
<i>Poseidonamicus viminea</i> (Brady, 1880)	Recent	Southern Ocean		Brady (1880), Benson (1972)
<i>Poseidonamicus riograndensis</i> Benson, 1983	Lower Miocene	DSDP site 92, S Atlantic		Benson & Peypouquet (1983)
<i>Poseidonamicus miocenica</i> Benson, 1983	Middle Miocene	DSDP site 92, S Atlantic		Benson & Peypouquet (1983)
<i>Poseidonamicus anteropunctatus</i> Whatley <i>et al.</i> , 1986	Miocene--Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus ocularis</i> Whatley <i>et al.</i> , 1986	Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus praenudus</i> Whatley <i>et al.</i> , 1986	Pliocene--Quaternary late Cenozoic	SW Pacific SW Pacific N Atlantic		Whatley <i>et al.</i> (1986) Whatley & Coles (1987)
<i>Poseidonamicus punctatus</i> Whatley <i>et al.</i> , 1986	Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus robustus</i> Whatley <i>et al.</i> , 1986	Eocene--Oligocene	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus rudis</i> Whatley <i>et al.</i> , 1986	Eocene--Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus</i> sp. Whatley <i>et al.</i> , 1986	Pliocene	Ita Mai Tai guyot, SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus</i> cf. <i>P. major</i> Benson, 1972	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> cf. <i>P. pintoii</i> Benson, 1972	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> sp. Whatley & Coles, 1987	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> sp. nov. Coles & Whatley, 1989	Oligocene	NE Atlantic		Coles & Whatley (1989)

TABLE 2  
Sample sites.

TBD	Latitude °S	Longitude °E	Depth (m)	No. ostracod valves	No. <i>P. panopsus</i>	Percentage <i>P. panopsus</i>	Percentage mud
Walvis Shelf							
3769	22,250	13,233	223	39	1	3	9,3
Orange Shelf							
2752	29,783	16,017	170	374	1	0,1	90,4
2973	28,417	15,000	173	1 460	1	0,1	82,4
2975	28,417	14,583	180	892	1	0,1	76,4
2925	28,900	15,367	183	284	3	1	25,8
2974	28,417	14,800	186	2 011	2	0,1	79,7
2840	30,917	15,700	205	108	9	8	8,7
2736	29,950	15,417	205	555	6	1	83
2717	30,400	16,433	218	112	4	4	33
2703	30,133	15,433	220	239	7	3	76,4
2485	30,917	16,000	227	114	2	2	19,6
2719	30,450	16,067	240	140	13	10	30,2
2361	31,313	16,858	241	70	9	13	64
2884	29,317	14,717	252	159	2	1	22
2691	30,533	15,617	265	43	1	2	27,4
2690	30,517	15,833	271	137	12	9	23
2460	31,233	16,625	272	39	1	3	90
2459	31,233	16,383	300	299	5	2	85,7
2976	28,417	14,383	350	18	2	11	92,5
2447	31,925	16,467	350	49	1	2	22,9
3577	31,367	16,083	453	96	1	1	84,2
SW Cape							
6823	34,093	18,215	120	1 098	11	1	—
3587	33,995	18,148	140	167	7	4	25,7
6825	34,090	18,173	160	222	10	5	—
1691	34,567	18,483	220	516	5	1	55
1694	34,750	18,327	425	31	1	3	72,4
1697	34,767	18,250	545	112	1	1	62

Phylum CRUSTACEA Pennant, 1777

Class OSTRACODA Latrille, 1806

Order PODOCOPIDA Müller, 1894

Suborder PODOCOPINA Sars, 1866

Superfamily CYTHERACEA Baird, 1850

Family *Trachyleberididae* Sylvester-Bradley, 1948

Subfamily *Thaerocytherinae* Hazel, 1967

Genus *Poseidonamicus* Benson, 1972

The genus was erected by Benson (1972) to accommodate a number of deep-sea, reticulate to virtually smooth, holamphidont-hinged species. They are characterized by certain features of their carapace morphology, such as the absence of an ocular rib, the presence of regular, vertically aligned fossae and muri posteromedianly, and a reticulate to punctate area medianly, the two areas being separated by a subvertical loop in the region of the adductor scars. These

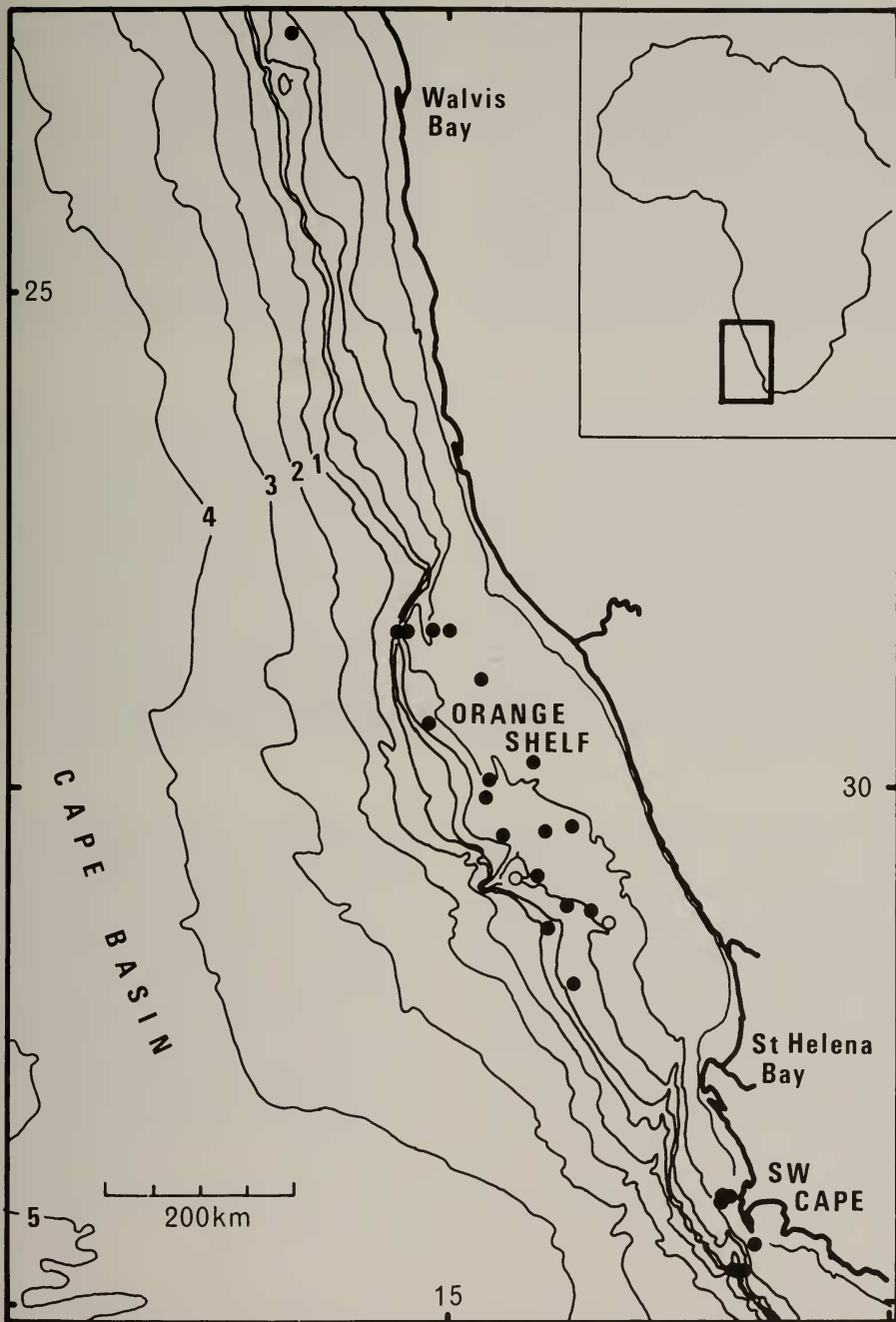


Fig. 1. Locations of sediment samples containing *Poseidonamicus panopsus* sp. nov. on the continental margin off south-western Africa. Isobaths at 100 m to 500 m and 1 km to 5 km. Sample numbers and locations are listed in Table 2. Open circles are sites with living specimens. Inset shows location of study area.

features are present even in smooth species, such as *P. nudus*, if viewed in transmitted light. Benson (1972) based the genus on five species (see Table 1; type species *P. major* Benson, 1972), and the diagnosis has been amended by Whatley *et al.* (1986) on the basis of their study of six additional species from the SW Pacific (Table 1).

*Poseidonamicus panopsus* sp. nov.

Figs 2-3, 4A-E, 5C

*Bradleya?* sp. Boomer, 1985: 42-43, pl. 3 (figs 35-36).

*Derivation of name*

Greek *panops*, all seeing. With reference to the well-developed ocular structures of this obviously sighted species, and also because Gods and their friends tend to be all seeing.

*Material*

- Holotype SAM-PQ-MF0502, female LV, TBD 2719, 240 m.  
 Paratypes SAM-PQ-MF0503, female LV, TBD 2719, 240 m.  
 SAM-PQ-MF0504, ?male RV, TBD 2690, 271 m.  
 SAM-PQ-MF0505, ?male LV, TBD 2459, 300 m.  
 SAM-PQ-MF0506, female carapace, TBD 2840, 205 m.  
 SAM-PQ-MF0507, juvenile LV, TBD 2840, 205 m.  
 SAM-PQ-MF0508, juvenile RV, TBD 6823, 120 m.

*Dimensions (mm)*

	<i>length</i>	<i>height</i>	<i>width</i>
MF0502	0,91	0,51	—
MF0503	0,89	0,52	—
MF0504	0,92	0,49	—
MF0505	0,89	0,48	—
MF0506	0,85	0,47	0,48
MF0507	0,64	0,37	—
MF0508	0,70	0,39	—

*Diagnosis*

A medium-sized, sighted species of *Poseidonamicus* with large hemispherical eye tubercle and distinct internal ocular sinus. Ornament reticulate with large open fossae, the solae of which are secondarily reticulate. SCT prominent; medianly inflated. Dorsal margin with prominent anterior and posterior hinge ears in LV.

*Description*

*External features.* Medium-sized (see relative size scale for genus, Whatley *et al.* 1986: 388), thick-shelled and robust. Subrectangular in lateral view; strongly inflated medianly and bluntly acuminate terminally in dorsal view. AM

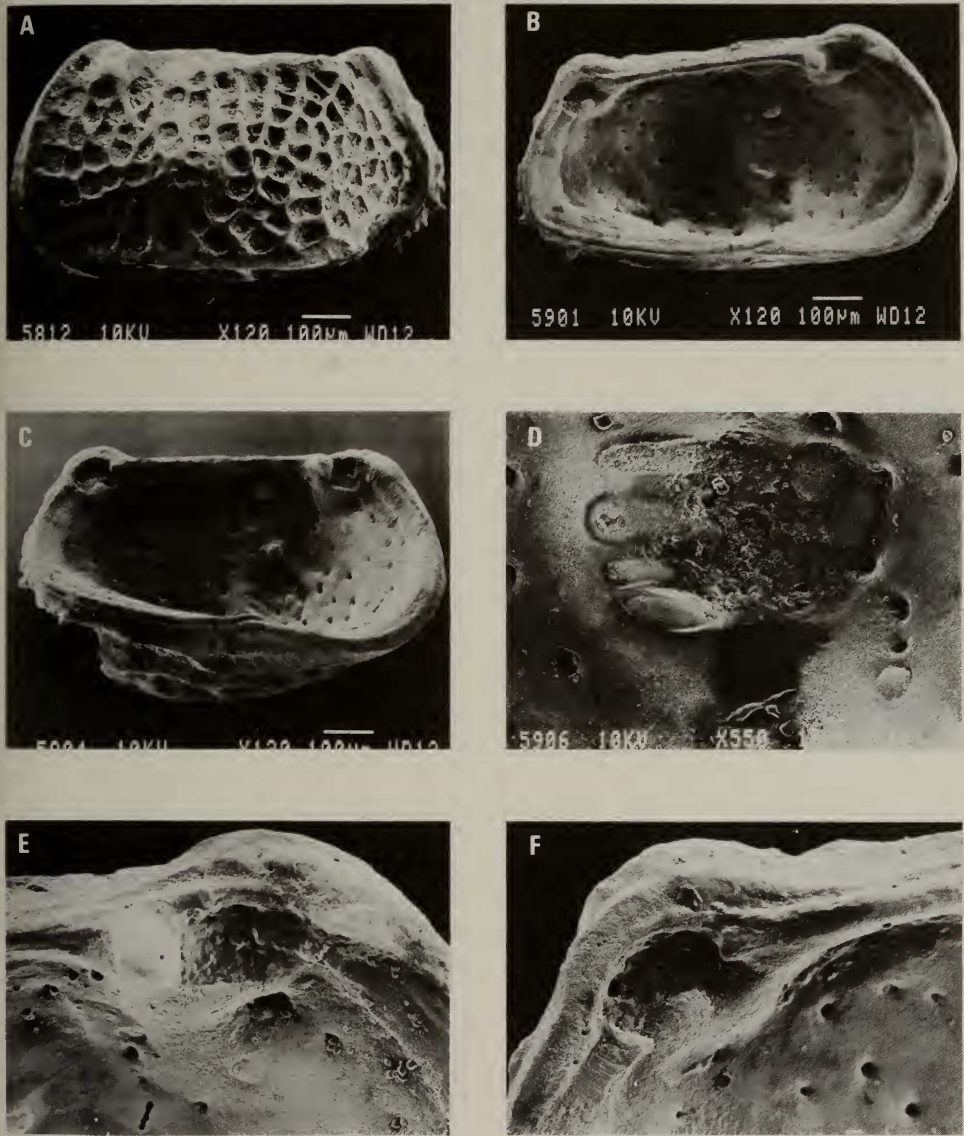


Fig. 2. *Poseidonamicus panopsus* sp. nov. SAM-PQ-MF0502, holotype, LV, female, TBD 2719, 240 m. A. External view. B. Internal view. C. Oblique internal view. D. Central muscle scars. E. ATE. F. PTE.

Scale bars: A-C = 100 microns; D-F = 10 microns.

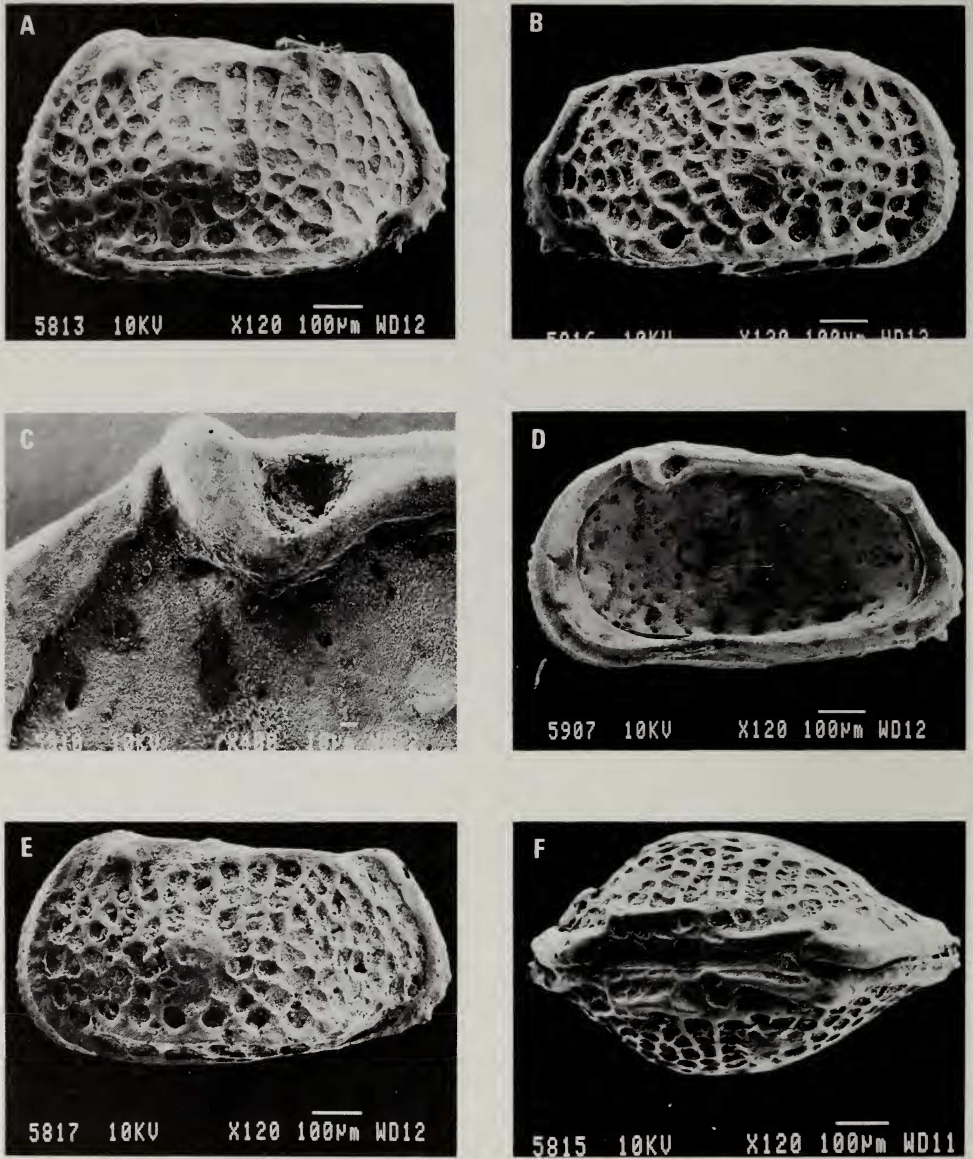


Fig. 3. *Poseidonamicus panopsus* sp. nov. A. SAM-PQ-MF0503, LV, female, TBD 2719, 240 m. B-D. SAM-PQ-MF0504, RV, male, TBD 2690, 271 m. B. External view. C. ATE. D. Internal view. E. SAM-PQ-MF0505, LV, male, TBD 2459, 300 m. F. SAM-PQ-MF0506, carapace, dorsal view, TBD 2840, 205 m. Scale bars: A-B, D-F = 100 microns; C = 10 microns.



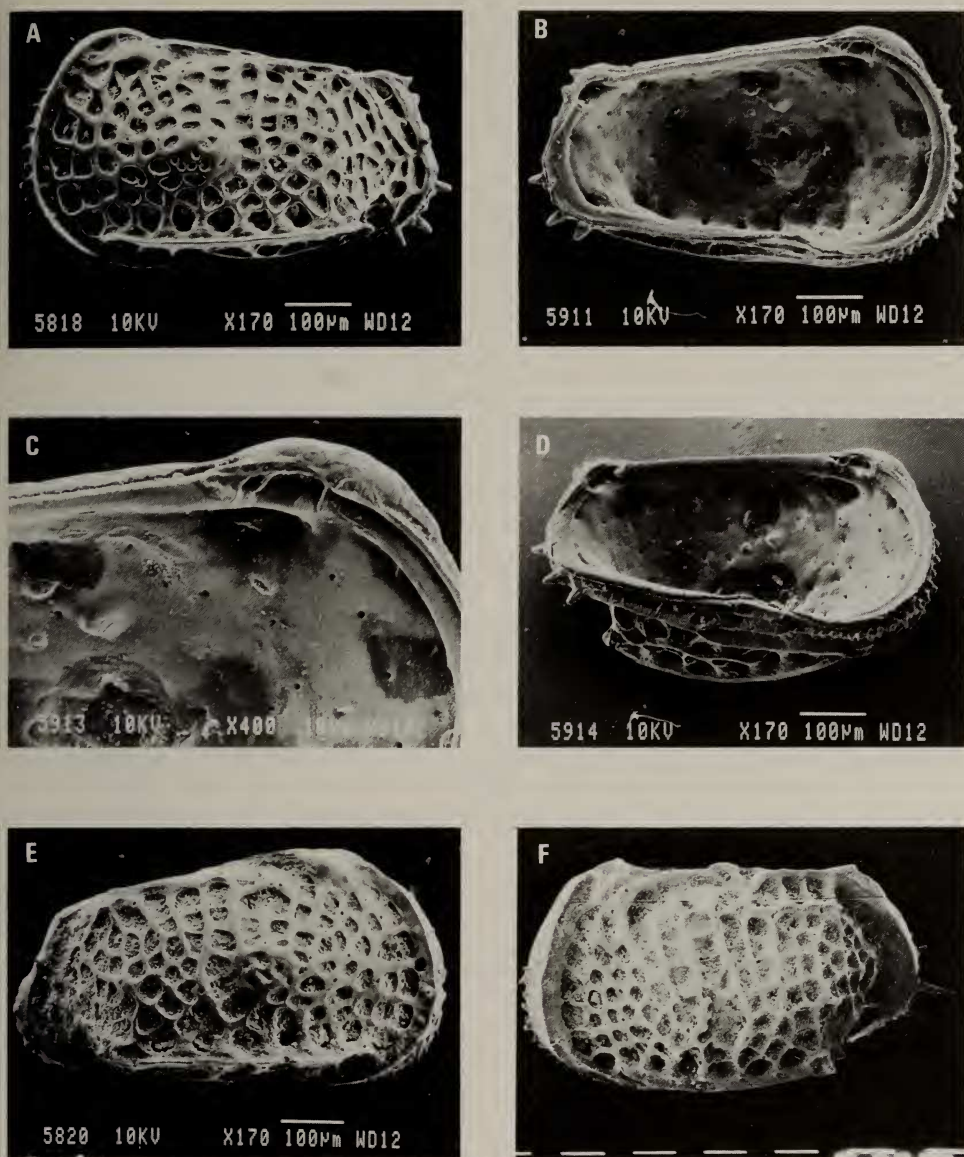


Fig. 4. A-E. *Poseidonamicus panopsus* sp. nov. A-D. SAM-PQ-MF0507, LV, juvenile, TBD 2480, 205 m. A. External view. B. Internal view. C. ATE. D. Oblique internal view. E. SAM-PQ-MF0508, RV, juvenile, TBD 6823, 120 m. F. *Poseidonamicus major* Benson, 1972, SAM-PQ-MF0495, LV, TBD 6851, 2 916 m, continental slope off south-western Africa. Scale bars: A-B, D-F = 100 microns; C = 10 microns.

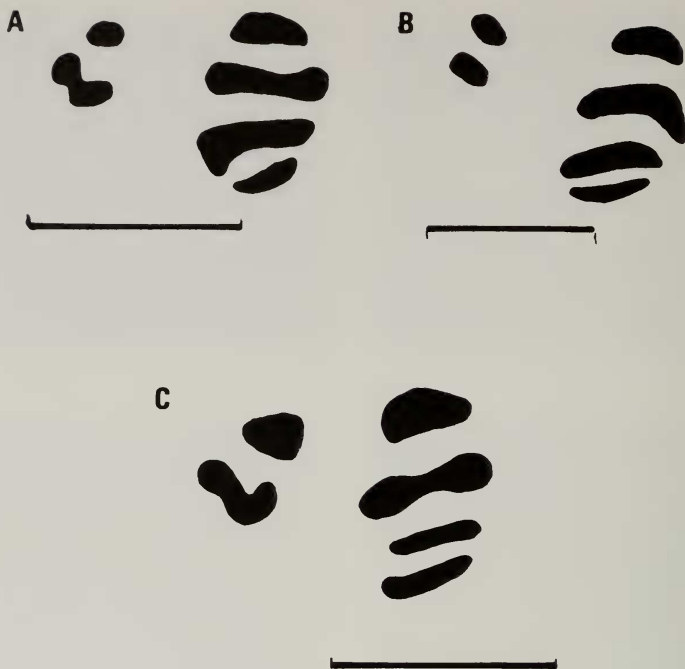


Fig. 5. Comparison of central MS patterns. A. *Poseidonamicus major* Benson, 1972, SAM-PQ-MF0497, RV, TBD 6851, 2 916 m, continental slope off south-western Africa (Dingle *et al.* in press). B. *Poseidonamicus major* Benson, 1972, USNM 174354, RV, IIOE 363B, 2 995 m, Mozambique Channel (Benson 1972). C. *Poseidonamicus panopsus* sp. nov. SAM-PQ-MF0504, RV, TBD 2690, 271 m.

Scale bars = 100 microns.

asymmetrically rounded in RV; with more pronounced antero-dorsal slope in LV; bearing numerous small marginal denticles. PM with blunt apex below mid-height and with short, convex denticulate postero-ventral slope and longer straight or concave postero-dorsal slope. DM straight with prominent anterior and posterior hinge ears in LV, particularly in the female. VM straight to very gently convex. Greatest height at the ACA, greatest length just below mid-height; greatest width just behind mid-length. Eye tubercle large, hemispherical and prominent, more peripheral in the RV than the LV due to the presence of the hinge ear in the latter. Ornament reticulate with large open fossae of fairly regular size, which are more circular anteriorly than elsewhere. Muri somewhat preferentially aligned vertically postero-dorsally, and horizontal to subradiate anteriorly. Solae secondarily reticulate in a radiate pattern. SCT slightly elevated in the region of the adductor scars, bearing small deep fossae and being embraced posteriorly and ventrally by the mural loop characteristic of the genus. Marginal rims prominent anteriorly and posteriorly; smooth except for a thin ridge along their crests. Vento-lateral ridge prominent and sub-ponticulate. A dorsal ridge, divided into two parts, extends subparallel to the dorsal margin.

*Internal features.* Calcareous inner lamella rather narrow, but strongly developed, selvage prominent. Avestibulate. Internal ocular sinus distinct, open in juveniles, somewhat restricted at its base in adults. Hinge holamphidont. MS comprising four undivided adductors, two frontals and two mandibular scars.

#### *Remarks*

This species differs from all other known species of the genus by possessing a prominent eye tubercle, a distinct internal ocular sinus, an inflated carapace, and in details of its ornamentation. The only other species of *Poseidonamicus* with ocular features is *P. ocularis* Whatley *et al.*, 1986. The latter species, from the Quaternary of three DSDP sites in the southern part of the area between Australia and New Zealand, was so named because it has a small (much smaller than that of *P. panopsus* sp. nov.) but prominent eye tubercle and an internal ocular sinus. The two species, despite the fact that they both possess strong hinge ears in the LV, can readily be distinguished in that they possess quite different ornament, and because *P. ocularis* lacks a SCT.

Although the external morphology of the new species differs significantly from *P. major* Benson and there is no possibility of confusion, we include a comparison of the central MS of the two species, because *P. major* is the only other representative of the genus recorded from southern Africa (Mozambique Channel, Benson 1972; Cape Basin, Dingle *et al.* in press). The MS of the two species are very similar (Fig. 5), with the anterior scars consisting of an ovate dorsal scar and a partially subdivided ventral scar, whereas the adductors are all elongate/ovate, with a 'dog's bone'-shaped second scar. The third scar of the adductor quartet in *P. major* is relatively longer than in *P. panopsus*.

#### *Range*

Pleistocene–Recent.

## DISCUSSION

The discovery of a sighted species of *Poseidonamicus* living on the continental shelf off south-western Africa has a number of important implications for understanding the evolution of the genus.

#### DISTRIBUTION AND ECOLOGY

*Poseidonamicus panopsus* sp. nov. has been found on the continental margin of south-western Africa between latitudes 22°S and 35°S, where it has a depth range of 120 m (mid-continental shelf) to 545 m (upper continental slope) (Fig. 1, Table 2). With the exception of sample TBD 3769 (NW of Walvis Bay), however, all the occurrences lie south of 28°S, and cluster into two distinct groups: on the Orange Shelf (28°S–32°S); and off the SW Cape (34°S–35°S). The isolated site off Walvis Bay consists of one valve, and this is separated by 6 degrees of latitude (650 km) from the Orange Shelf population.

TABLE 3

Distribution of *Poseidonamicus panopsus* sp. nov. (values are means for n sites).

Area (n)	Percentage <i>P. panopsus</i>	Percentage mud	Depth (m)	Range
A. Walvis Shelf (1)	3	9	223	223
B. Orange Shelf (20)	4	56	248	170-453
C. SW Cape (6)	3	54*	268	120-545
D. Overall (27)	3	53*	251	120-545

Living specimens occur at two sites on the Orange Shelf. At these sites the following parameters apply:

Percentage <i>P. panopsus</i>	Percentage mud	Depth (m)
8	9	205
13	64	241

\* = excludes samples 6823 and 6825 for which no mud values are available.

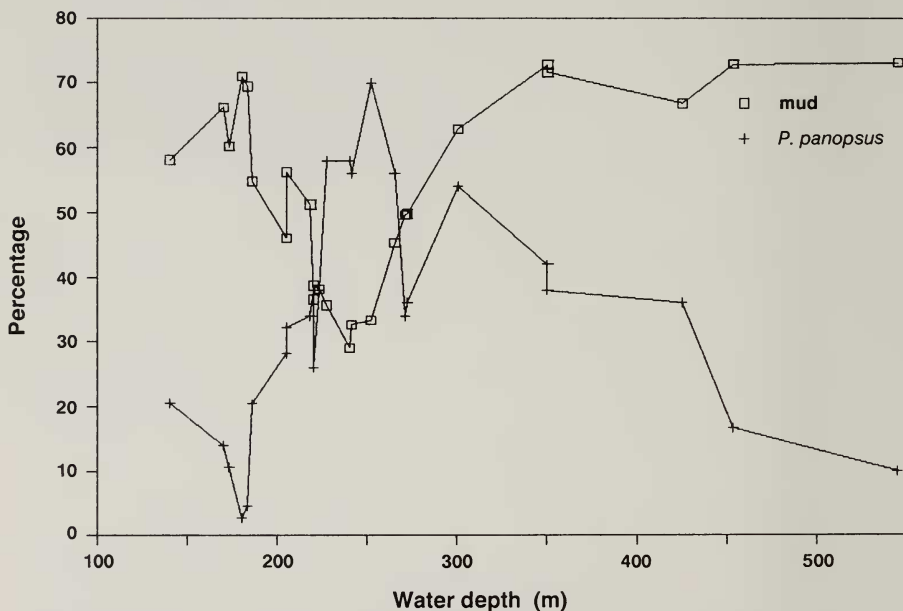


Fig. 6. Mud content of sediment samples and relative abundance of *Poseidonamicus panopsus* sp. nov. (percentage of ostracod fauna  $\times 10$ ) plotted against water depth. Mud and percentage ostracod values are smoothed 5-point means. Samples TBD 6823 and TBD 6825 have not been included (no analysis of mud contents are available). Note the inverse relationship between the mud content and percentage *P. panopsus*, with peak values of the latter on the outer continental shelf (c. 250 m water depth).

Table 3 lists some of the parameters of the areas of occurrence. In the Orange Shelf and SW Cape populations, the species has a similar depth range (170–453 m, and 120–545 m, respectively), and the mean mud contents of the sediments in which the species is recorded (53% and 54%) and the mean abundance of the species (4% and 3%) are also very close. These two areas are separated by approximately 200 km of shelf which is barren of *P. panopsus*. Plots of the abundances of the species (as percentage of the ostracod population) against the mud contents of the sea-floor sediments (Fig. 6) indicate that the species peaks (up to 60% total ostracod population) at about 250 m water depth, where the mud content of the sediment is lowest (mean of 30%). On the adjacent inner shelf and outer shelf/upper slope, where the mean mud contents are >60%, the abundance of *P. panopsus* rapidly declines. This indicates that the species is generally not tolerant of high mean mud values (>70%). However, the fact that the region between the Orange Shelf and SW Cape populations, which is barren of the species, has a mean mud content of 30 per cent (compared to 50% for all sediments in the two populated areas) suggests that a minimum mean mud threshold (30%) is one of the factors necessary to sustain the species.

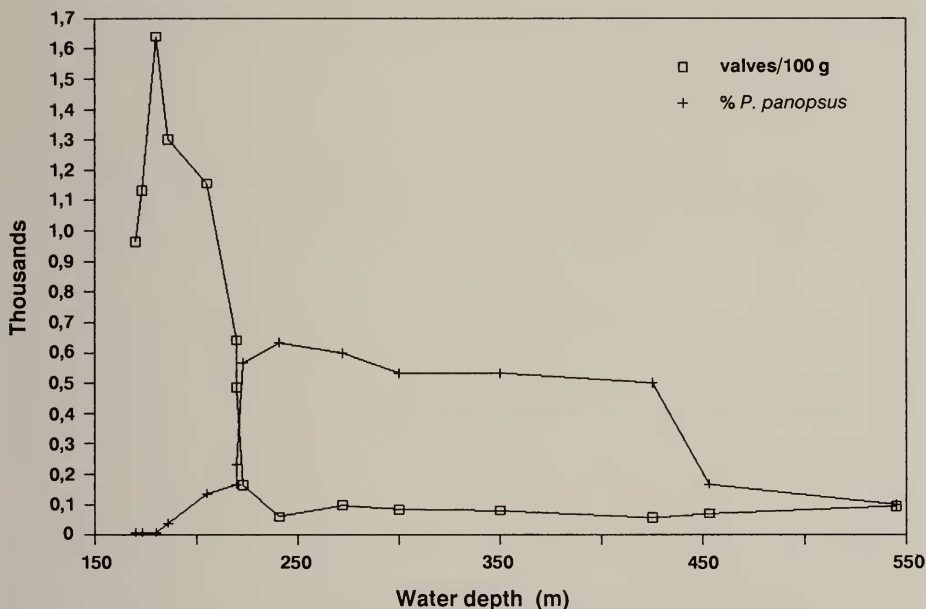


Fig. 7. Abundance of ostracod population (number of valves/100 g sediment) and relative abundance of *Poseidonamicus panopsus* sp. nov. (percentage of ostracod fauna  $\times 100$ ) plotted against water depth. Ostracod population and *P. panopsus* values are smoothed 3-point means. Samples TBD 6823 and TBD 6825 are not included (no ostracod population abundance values available). Note the high ostracod population values on the mid-shelf, which decline rapidly into deeper water, with a concomitant increase in relative abundance of *P. panopsus*.

A further limiting factor within the two main *P. panopsus* population centres is the abundance of the whole ostracod fauna (Fig. 7). Mean values (measured as number of valves/100 g of original dry sediment) peak on the inner shelf (>500 valves/100 g in <200 m water depths), and fall rapidly towards the outer shelf and slope. Concomitant with this decline in the overall abundance of the ostracod fauna, there is a marked increase in the percentage of this fauna made up by *P. panopsus*. This trend suggests that the species has limited toleration of competition from large numbers of individuals belonging to other species, although at present the nature of this factor remains unknown.

Living specimens were collected at two locations (TBD 2840 and 2361), both in the Orange Shelf area, but plots of the population structure show that in both this area, and within the SW Cape occurrences, the mean percentages of adult valves varies between 20 and 70 per cent, with the higher values concentrated in water depths between 200 m and 250 m in the Orange Shelf area (Figs 8, 9). These assemblages of mixed adults and juveniles suggest that both the main areas of occurrence reflect viable extant populations. The isolated site off Walvis Bay is a single dead adult valve, and we are not in a position to determine its true status. Its transportation as a relatively fragile clast 650 km from the the Orange Shelf population seems unlikely, but we have good sample coverage over the whole of the adjacent continental shelf, and it is equally unlikely that a population centre larger than 300 km<sup>2</sup> would have been undetected.

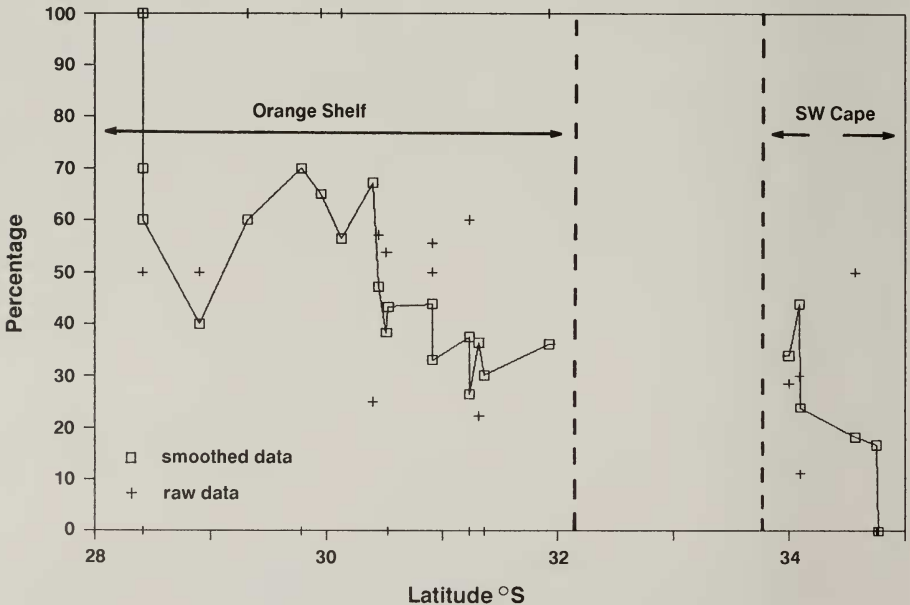


Fig. 8. Percentage of adult valves of *Poseidonamicus panopsus* (raw and smoothed 5-point means) plotted against latitude. Sample TBD 3769 off Walvis Bay is omitted. Mean values: Orange Shelf = 49 per cent adult, SW Cape = 29 per cent adult.

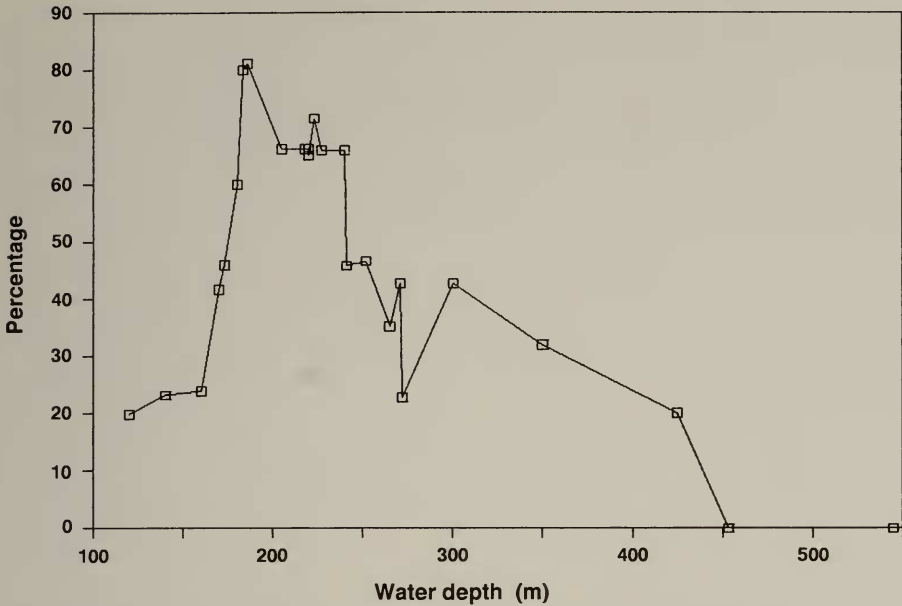


Fig. 9. Percentage of adult valves of *Poseidonamicus panopsus* (smoothed 5-point means) plotted against water depth. Note that peak values (>60%) lie around 200 m water depth, which is slightly shallower than the peak values of abundance of the species (Fig. 6—250 m).

The three deepest sites at which the species was recovered (TBD 1694, 425 m; TBD 3577, 453 m; and TBD 1697, 545 m) all consist of single juvenile valves, which possibly indicate allochthonous occurrences due to downslope postmortem transportation. If this is the case then the true lower depth limit of the species is 350 m.

The oceanographic climate off south-western Africa is complex, with large-scale upwelling over the continental shelf area (Shannon 1985). Figure 10 shows sea-floor variations in temperature, salinity, and dissolved oxygen across the continental margin at the southern end of the Orange Shelf (32°S). The upper depth limit of *P. panopsus* on the Orange Shelf is 170 m, and this occurs at approximately the same depth as two important changes in physico-chemical parameters: the base of the inner shelf thermocline (c. 13°C—<9.5°C), and the western limit of the continental shelf low dissolved oxygen zone. The slightly shallower upper depth limit (120 m) off the SW Cape (34°S) may reflect somewhat lower sea-floor temperatures at shallower depths: the 9°C isobath intrudes to depths of 100 m for much of the year in this area (see Shannon 1985, fig. 21).

Low dissolved oxygen values (<2 ml/l) may also be important limiting factors in the latitudinal distribution of the species. A major source of oxygen deficient water lies to the north of the Orange Shelf, where Chapman & Shannon (1985)

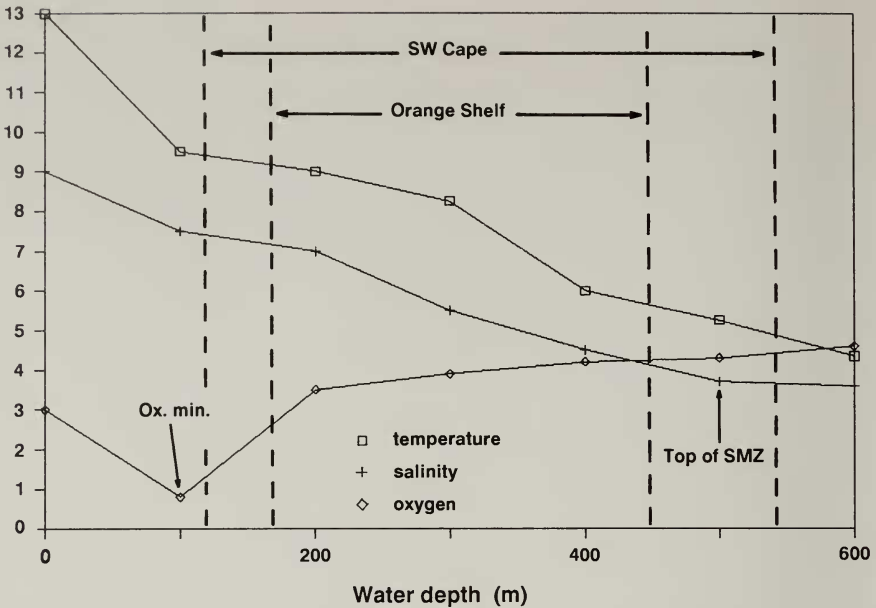


Fig. 10. Variations in water temperature, salinity, and dissolved oxygen on the sea floor along a transect across the continental margin at approximately 32°S. Data from Fuglister (1960), Stander (1964), Shannon (1966, 1985), Shannon & Van Rijswijk (1969). Depth ranges of *P. panopsus* on the Orange Shelf and off the SW Cape are indicated by arrows. Note that the western limit of the 'oxygen deficient zone' (<2 ml/l, as defined by Chapman & Shannon 1985) lies at approximately 180 m water depth (Stander 1964). This is somewhat deeper than predicted by the straight line connecting the two data points used to create the dissolved oxygen curve.

Parameters: temperature = °C, salinity =  $[(\text{‰} - 34) \times 10]$ , dissolved oxygen = ml/l. Abbreviations: oxygen = dissolved oxygen, Ox. min. = oxygen minimum, SMZ = salinity minimum zone of AAIW.

identified a double low on the continental shelf, whereas a smaller, but persistent source is centred on St Helena Bay. We suspect that the latter may contribute to the *P. panopsus*-barren region between 32°S and 34°S. Similarly, the oxygen-low area immediately off the Orange River mouth (Chapman & Shannon 1985, fig. 6) may be a factor restricting the species to water deeper than 170 m on the Orange shelf (compared to 120 m off the south-western Cape).

At the lower depth limit (545 m or 350 m, depending on whether our three deepest specimens are allochthonous), gradients in the variation of sea-floor temperature and dissolved oxygen are relatively low, but Shannon (1985) has located the top of the salinity minimum zone (SMZ) within the Antarctic Intermediate Water mass (AAIW) at approximately 600 m along most of the continental margin of south-western Africa. Data in Fuglister (1960) show this phenomenon to be closer to 500 m at 32°S (Fig. 10), and Dingle *et al.* (in press) have recognized the bottom of the SMZ (at about 950 m) to be a major faunal barrier, separating neritic and bathyal ostracod faunas. We suspect that the lower



depth limit of *P. panopsus* is regulated by the level of the top of the SMZ within the AAIW mass.

In summary, we believe that the following environmental parameters influence the distribution of *Poseidonamicus panopsus* sp. nov.:

1. The species prefers a mud content in the sediment of between 30 and 50 per cent, with the lower value limiting its distribution.
2. It is most abundant where it lives within ostracod populations with low abundances (<400 valves/100 g).
3. Limiting water temperatures are approximately 9,0°C–5,8°C.
4. Limiting salinities are 34,70–34,40‰.
5. Limiting dissolved oxygen values are 2,7–4,2 ml/l.
6. The species tolerates the nutrient-rich conditions of the upwelling cells associated with the Benguela system, but where these cells result in intense biological productivity and oxygen deficiencies in the water column (to the north of the Orange Shelf area, and between the Orange Shelf and the SW Cape area), dissolved oxygen values on the sea floor are too low for its survival.

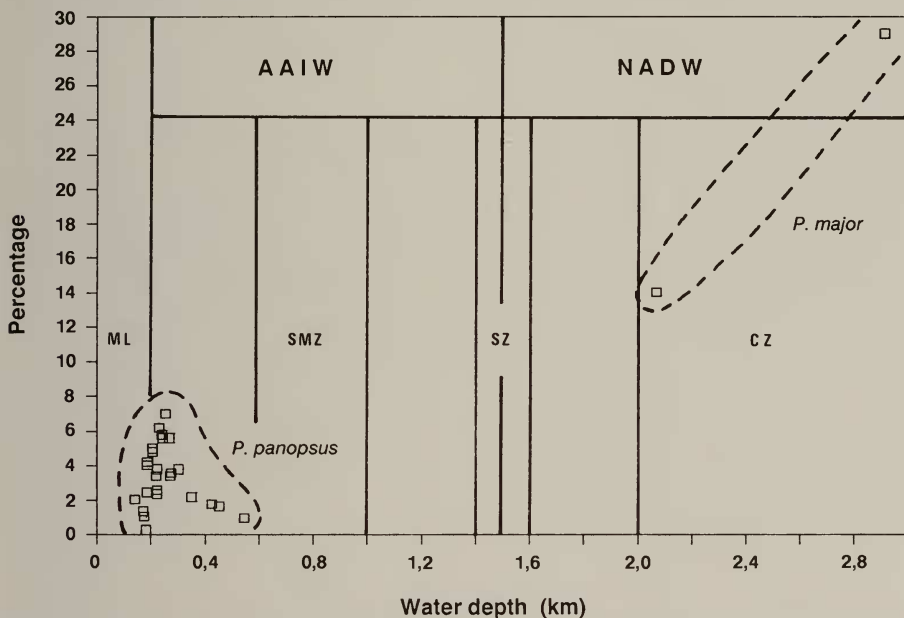


Fig. 11. Relative abundances of *Poseidonamicus panopsus* sp. nov. and *Poseidonamicus major* Benson (percentage of ostracod population) plotted against water depth. The populations of the two species are separated by 1 500 m of water on the continental slope which contains the following physico-chemical barriers: salinity minimum zone of the Antarctic Intermediate Water mass; the shear zone of the Antarctic Intermediate Water/North Atlantic Deep Water masses boundary; and the top of the core of the North Atlantic Deep Water. Note also that *Poseidonamicus major* is a more important component of the abyssal ostracod fauna than is *P. panopsus* of the neritic ostracod fauna (means 22% and 3,3%, respectively).

Abbreviations: AAIW = Antarctic Intermediate Water; CZ = core zone; ML = mixed layer; NADW = North Atlantic Deep Water; SMZ = salinity minimum zone; SZ = shear zone.

Dingle *et al.* (in press) discuss some of the factors that may be responsible for confining various deep-water (>950 m) ostracod assemblages to their respective depth ranges. They concluded that the upper depth limit of *P. major* off south-western Africa is probably controlled by the position of the top of the core zone of the North Atlantic Deep Water mass (NADW), above which higher temperatures (>3,0°C) and lower salinities (<34,86‰) occur. Figure 11 shows the depths and abundances (as percentage of ostracod fauna) of samples containing *Poseidonamicus major* and *P. panopsus* off south-western Africa and emphasizes that, although the two species are both extant, they are separated by 1 500 m of water column that contains two major barriers to faunal mixing: the SMZ of the AAIW; and the contact zone between the AAIW and the NADW. As Dingle *et al.* (in press) point out, both these are powerful barriers that control the Neritic/Upper Bathyal, and Upper Bathyal/Lower Bathyal faunal boundaries, respectively. In addition, the top of the NADW core regulates the Lower Bathyal/Abyssal faunal boundary. Because the water masses that give rise to the controlling physico-chemical gradients have been in existence since at least mid-Tertiary time, the separation of the two *Poseidonamicus* species off south-western Africa is likely to have been a long-term phenomenon.

#### GENERAL CONSIDERATIONS

Benson (1972: 21), apart from speculating that the ancestry of *Poseidonamicus* 'reaches far back into the Cretaceous', could not, at the time, suggest a possible ancestor for the genus. Subsequently, Whatley *et al.* (1983) suggested that it evolved in the area of the SW Pacific Ocean, and more particularly in the region between Australia and New Zealand, where they encountered it in DSDP samples dating back to the Lower Eocene. The two oldest species that they found in the Lower Eocene, *P. rudis* and *P. robustus* (Whatley *et al.* 1986), were shown to exhibit a considerable resemblance to certain Upper Cretaceous taxa from western Australia. These authors (1983: 497, fig. 2) suggested that *Hermanites sagitta* Bate, 1972, from the Campanian of the Carnarvon Basin, or some similar species, could be the ancestor of *Poseidonamicus*. They argued that *H. sagitta* could have given rise to the hypothetical ancestral *Poseidonamicus* species, which would probably have been sighted, but which gave rise, once the genus had been involuntarily inducted into the deep sea, to all the blind species in the deep-water environments of the world's oceans. Since the two Australian Lower Eocene species are blind (a characteristic of all podocopid ostracods living in waters deeper than about 500 m) then this induction must have taken place at some stage prior to the Eocene.

The same authors suggested, however (1983: 479, fig. 2; 1986: 391), that *P. ocularis* evolved from a fully sighted, shallow, shelf-dwelling ancestor in the Quaternary. *Poseidonamicus ocularis* was only recovered from bathyal environments in the southern part of the area between Australia and New Zealand (DSDP sites 207, 277 and 281) and only from Quaternary strata. They argued (1983: 479) that the discovery of *P. ocularis* 'implies that there has persisted in

shallow waters of this area until recent times a population with eyes, derived direct from a postulated sighted ancestor'. They also comment on the 'exciting prospect that a living sighted species of the genus may be encountered in due course'.

The discovery of the sighted shelf species *P. panopsus* sp. nov. has justified these expectations, but the present authors admit to surprise that it should have been encountered off the southern African Atlantic coast rather than in Australasian waters. Given the Quaternary age of *P. ocularis*, however, it remains quite conceivable that a shallow-water shelf species of the genus remains to be discovered living in the antipodes.

In logic, *P. panopsus* must be considered a lineal descendant of a late Cretaceous or early Palaeogene hypothetical sighted ancestral *Poseidonamicus* species that subsequently give rise to all the blind deep-water and sighted shallow-water species of the genus. Direct contiguity of continental shelf environments between what is now southern Africa and Australasia probably ceased at about 100 m.y. BP (Albian), when southern Africa finally separated from the Falkland Plateau extension of South America (see Dingle *et al.* 1983). Circuitous shallow-water connections probably continued until Turonian times via the Walvis Ridge/Rio Grande Rise archipelago across the South Atlantic, and the Drake Passage shallows between South America and Antarctica but, since the latter date, the two areas have been separated by barriers of abyssal depths. Consequently, the ancestry of *Poseidonamicus panopsus* is uncertain, given the fact that the genus probably arose in Australasia from shallow-water Upper Cretaceous stock. Dingle (1981) discussed the similarity between southern African and western Australian Campanian shallow-water ostracods, and recorded a relatively high similarity (27%) at the generic level. However, there were no species in common, and no evidence suggests any contact between the ostracod populations since at least the mid-Cretaceous. *Hermanites kennedyi* Dingle (Campanian) from SE Africa is similar to *H. sagitta* Bate, a possible progenitor for the SW Pacific *Poseidonamicus* populations (Whatley *et al.* 1983), but even the possibility of homeomorphy from a similar ancestor is not attractive, because there is no record of *Poseidonamicus* in the Tertiary of southern Africa. A lineal connection with the Australasian stocks seems the most likely solution, but it may be that *P. panopsus* or its ancestors do not have a long history on the continental margin of southern Africa, and migrated into the area relatively recently (?late Tertiary) from other areas (such as eastern Africa). Whatever the case, it is remarkable that sighted species have survived so long apart (to the Recent in southern Africa, and to at least the Pleistocene in Australasia) without either becoming extinct or being subject to major evolutionary change. Although this can only be confirmed if and when sighted shelf species of *Poseidonamicus* are recovered from Tertiary shallow-water deposits in the Southern Hemisphere, it does suggest that, when compared to the considerable degree of evolutionary change experienced by deep-water species (Whatley 1985), the genus has been more stable in shallow environments.

## ACKNOWLEDGEMENTS

RVD gratefully acknowledges research facilities provided by Drs M. A. Cluver and Q. B. Hendey at the South African Museum, and Dr A. R. Lord at University College, London. The samples were collected whilst RVD was in the Marine Geoscience Unit at the University of Cape Town, and the University, the South African National Committee for Oceanographic Research, and the Foundation for Research Development are thanked for funding sea-time. The authors are grateful to the Editorial Board of UCT and the South African Museum for subventing publication costs.

## REFERENCES

- BATE, R. H. 1972. Upper Cretaceous ostracods from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology* 10: 1-85.
- BENSON, R. H. 1972. The *Bradleya* problem, with descriptions of two new psychrospheric genera, *Agrenocythere* and *Poseidonamicus* (Ostracoda: Crustacea). *Smithsonian Contributions to Paleobiology* A12: 1-138.
- BENSON, R. H. & PEYPOUQUET, J. P. 1983. The upper and mid-bathyal Cenozoic ostracode faunas of the Rio Grande Rise found on Leg 72, Deep Sea Drilling Project. In: BARKER, P. F. *et al.* *Initial Reports of the Deep Sea Drilling Project 72*: 805-818. Washington: U. S. Government Printing Office.
- BOOMER, I. 1985. A reconnaissance survey of Recent and Holocene Ostracoda from the continental shelf of South West Africa. Unpublished M.Sc. thesis, University College, London. 98 pp.
- BRADY, G. S. 1880. Report on the Ostracoda dredged by 'HMS Challenger' during the years 1873-1876. *Report of the Scientific Results of the Voyage of HMS Challenger* (Zoology, 1) 3: 1-184.
- COLES, G. & WHATLEY, R. C. 1989. New Palaeocene to Miocene genera and species of Ostracoda from DSDP sites in the North Atlantic. *Revista Española de Micropaleontología* 21 (1): 81-124.
- CHAPMAN, P. & SHANNON, L. V. 1985. The Benguela ecosystem. Part II. Chemistry and related processes. *Oceanography and Marine Biology Annual Review* 23: 183-251.
- DINGLE, R. V. 1981. The Campanian and Maastrichtian Ostracoda of south-east Africa. *Annals of the South African Museum* 85 (1): 1-181.
- DINGLE, R. V., LORD, A. R. & BOOMER, I. In press. Deep-water Quaternary Ostracoda from the continental margin off south-western Africa (SE Atlantic Ocean). *Annals of the South African Museum*.
- DINGLE, R. V., SIESSER, W. G. & NEWTON, A. R. 1983. *Mesozoic and Tertiary geology of Southern Africa*. Rotterdam: Balkema.
- FREWIN, J. 1987. Palaeogene ostracods from the South African continental shelf. Unpublished M.Sc. thesis, University of Cape Town. 171 pp.
- FUGLISTER, F. C. 1960. *Atlantic Ocean atlas of temperature and salinity profiles and data from the International Geophysical Year of 1957-1958*. Woods Hole: Woods Hole Oceanographic Institution.
- SHANNON, L. V. 1966. Hydrology of the south and west coasts of South Africa. *Investigational Report Division of Sea Fisheries, South Africa* 58: 1-22.
- SHANNON, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology Annual Review* 23: 105-182.
- SHANNON, L. V. & VAN RIJSWIJCK, M. 1969. Physical oceanography of the Walvis Ridge region. *Investigational Report Division of Sea Fisheries, South Africa* 70: 1-19.
- STANDER, G. H. 1964. The Benguela Current off South West Africa. *Investigational Report Marine Research Laboratory, South West Africa* 12: 1-43.
- WHATLEY, R. C. 1983. Some aspects of the palaeobiology of Tertiary deep-sea Ostracoda from the S.W. Pacific. *Journal of Micropalaeontology* 2: 83-104.

- WHATLEY, R. C. 1985. The evolution of the ostracod genera *Bradleya* and *Poseidonamicus* in the deep sea Tertiary and Quaternary of the South-West Pacific. *Special Papers in Palaeontology* 33: 103-116.
- WHATLEY, R. C. & COLES, G. 1987. The late Miocene to Quaternary Ostracoda of Leg 94, Deep Sea Drilling Project. *Revista Española de Micropaleontología* 19 (1): 33-97.
- WHATLEY, R. C., DOWNING, S. E., KESLER, K. & HARLOW, C. J. 1986. The ostracod genus *Poseidonamicus* from the Cainozoic of D.S.D.P. Sites in the S.W. Pacific. *Revista Española de Micropaleontología* 18 (3): 387-400.
- WHATLEY, R. C., HARLOW, C. J., DOWNING, S. E. & KESLER, K. 1983. Some observations on the origin, evolution, dispersion and ecology of the genera *Poseidonamicus* Benson and *Bradleya* Hornibrook. In: MADDOCKS, R. F. ed. *Applications of Ostracoda, Proceedings of the Eighth International Symposium on Ostracoda*, Houston, 1982: 51-77.